A KEY TO THE GENERA OF THE MENOPONIDAE (AMBLYCERA : MALLOPHAGA : INSECTA)

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A KEY TO THE GENERA OF THE MENOPONIDAE (AMBLYCERA : MALLOPHGA : INSECTA)

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SYNOPSIS

A review of the characters which have been used in the diagnosis of the genera of the Menoponidae is given, together with a number not previously used. A discussion of their taxonomic value is included, followed by a key to the genera and subgenera of the family.

PART I

INTRODUCTION

In formulating a key to the genera of the Menoponidae an attempt has been made to use characters which not only define each genus but also place at least some of the genera in larger groupings; these may prove in some cases to be phylogenetic. The greater number of species now available has shown that many of the former key characters cannot always be used or have only a limited application. These include presence or absence of postpalpal and anteroventral head processes; ctenidia on the 3rd femur and sternites; asters of spiniform setae on sternite II of *Myrsidea*; subdivisions of the flagellum; number of prosternal setae; shape of head and abdomen; the characters of the dorsolateral margin of the head and hypopharyngeal sclerites. These characters may vary within groups of otherwise similar species or may be common to otherwise dissimilar genera. It is hoped that this key may give a clearer conception of the generic characters and their reliability in the taxonomy of the family. Only those structures of ectodermal origin and which can be seen satisfactorily without sections have been considered; the task of sectioning and examining a sufficient number of specimens of each genus would have been impossible and a number of the genera are represented only by specimens mounted on slides. Some characters have obviously been missed; also omitted are those which could not be seen clearly in all the available material or the morphology of which could not be correctly interpreted. There are also other characters which need further material and time for study, such as the segments and sensilla of the flagellum.

There follows a review of the characters of various parts of the body with a discussion of their taxonomic importance. These characters fall into four groups: those which are found throughout the Menoponidae and which are of little interest here, but are mentioned when they have been or might be included in generic descriptions; those which vary throughout a genus and are of specific value only; those which can be used for generic separation; and those which group similar genera together. The same character can of course be specific in one group and generic in another. Two cases have been found in which a character, apparently unique for the Amblycera, is of no more than specific or of species-group value (see *Comatomenopon elbeli* Emerson abdomen and *Meromenopon* head setae). It is appreciated that the term 'generic character' is not very meaningful considering how the generic concept

differs among workers on Mallophaga at the present time; elsewhere (Clay, 1947 : 457–477; 1951 : 171–175; 1953 : 581; 1966 : 332–333) the present writer's views on the genus have been made clear and need not be repeated. It is felt that at present there is little to be gained by attempting to group the genera into various families and other divisions.

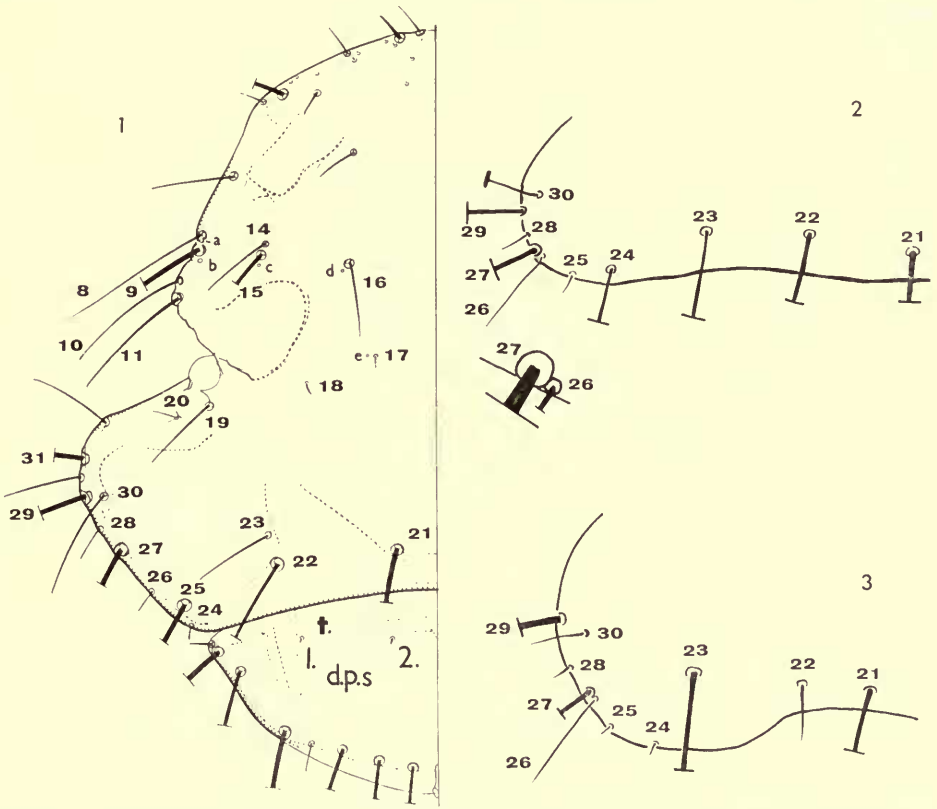
Head

1. *The Head Capsule.* The basic structure of the head is similar throughout the Menoponidae (Buckup, 1959; Haub, 1967), but the form of the dorsolateral margin (Text-fig. 4) and its junction with the temple margin, the presence or absence of a preocular notch or slit, position of the eyes and the form of the antennary fossa provide useful generic characters. The presence or absence of a narrow preocular slit is usually constant in a group of otherwise similar species, but in *Menopon* there is variation from a deep narrow slit (*M. interpositum* Ansari) to a shallow narrow slit (*M. gallinae*) to an approximately straight margin (*M. jellisoni* Emerson). *M. interpositum*, for instance, with the abdominal characters typical of *Menopon* has the dorsolateral margin of the head similar to that of *Amyrsidea perdicis*. Variously developed ventral sclerotized processes arising near the anterolateral margin may be present or absent (e.g. *Pacifimenopon* Price) or occasionally present in genera in which such processes are not usually found (e.g. *Machaerilaemus raggianae* Price & Emerson, *Kurodaia quatei* Price); they are probably of little phylogenetic value. Processes arising near the base of the maxillary palp (postpalpal processes, Text-fig. 5) are usually more constant within genera, but may be present or absent in *Nosopon* and *Pseudomenopon*, for example; in the latter genus and in *Colimenopon* they may be present in the nymph and absent in the adult; it is also doubtful whether their presence or absence forms good generic characters for some of the species infesting the Galliformes. The presence of these processes is therefore only specific in some genera, but in others is probably generic (e.g. *Kelerimenopon*, *Apterygon* Clay and *Hohorstiella*). The gular region has two or more setae each side and may or may not have a well-sclerotized plate; the form of this plate is a generic character in *Pseudomenopon* and *Colimenopon*.

The tentorium has been described by Symmons (1952 : 365) who showed its similarity in the species of Menoponidae she examined belonging to the genera *Colpocephalum*, *Menopon*, *Menacanthus*, *Myrsidea* and *Ancistrona*. In mounted specimens it is generally possible to see the anterior and posterior pits, the anterior tentorial arms and the tentorial bridge; differences are shown in the width of the bridge relative to the size of the head and the size of the posterior pits, but it is doubtful whether these will provide useful characters for the recognition of genera. In *Eureum* and *Dennyus* the bridge is narrowed centrally, but in some species this tends to be rather wider and would probably grade into that of some species of *Myrsidea*, for instance, which is broader than is usual in *Dennyus* but less broad than in some species of other genera. Symmons (1952 : 375) showed that there were some differences in the tentorium of *Trinoton*, mainly of muscle attachments, and of *Piagetiella*, in which parts of the bridge and anterior arms are difficult to see owing to some lack of sclerotization and to the heavy sclerotization of parts of the head.

The degree of pigmentation of the internal carinae gives a characteristic appearance to the head and may be correlated with other characters to help in generic groupings. However, it seems to be a rather variable character; the quill-inhabiting species, for instance, having a tendency to lighter pigmentation (e.g. *Comatomenopon*).

2. *The Head Setae and Sensilla.* These tend to form constant patterns (Clay, 1960 : 573) and the dorsal head setae expecially may be useful for the recognition



FIGS. 1–3. 1, Menoponidae head (dorsal) and pronotum, 2–3, Posterior part of dorsum of head. 2, *Menacanthus stramineus*. 3, *Colpocephalum* sp. *a-e*. dorsal head sensilla; 8–31. dorsal head setae; *d.p.s*. central pronotal setae 1–2; *t. transverse* pronotal carina.

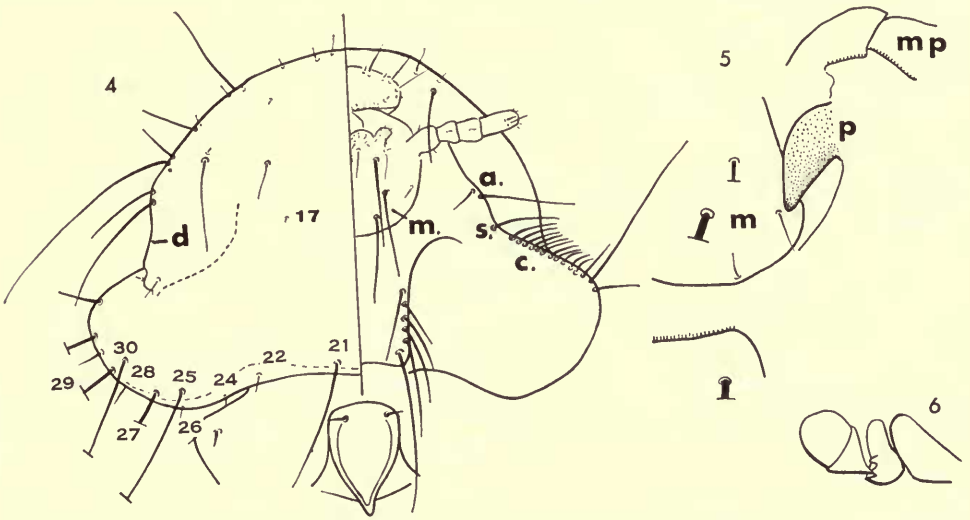
of genera and generic groupings. They have been used extensively in the key, being referred to by numbers e.g. seta 23; those of taxonomic importance have been labelled in Text-figs. 1–4. On the anterior region of the dorsum there may be extra setae in some species of a genus or in one sex only and the setae of this region have not therefore been used. The lengths of 10 and 11 (the preocular setae) are useful specific characters; the addition of one or more setae to this pair may be specific (*Actornithophilus crinitus* Clay) or generic (*Meromenopon*). *Ancistrona* has a row of fine setae along the inner dorsolateral margin (Text-fig. 20) not seen in any other

genus. Numbers 14–16 (setal complex and dorsal seta of Price & Beer, 1963 : 851) usually form a characteristic group, their position in relation to each other often being of specific importance. The size and position of 17 and 18 (the mid-dorsal head setae) may form generic (*Cuculiphilus*) or specific characters (e.g. *Colpocephalum*); the absence of 18 is a generic character in *Myrsidea*. The two ocular setae (19 and 20) seem to be always present: 19 usually lies near the division of the two ommatidia (when apparent); 20 is usually small and often marginal and difficult to see; in *Dicteisia* it is well developed (Price, 1968). The posterior marginal or submarginal temporal and occipital setae are numbered from the centre outwards as the first ten form useful taxonomic characters, whereas the anterior temporal setae are not always constant in number, and in mounted specimens may get confused with the ventral. The occipital setae (21–22) are always present and their relative length and thickness may form specific or generic characters. Seta 23 may lie anterior or anterolateral to 22 (Text-fig. 1) or in a straight line with 21 and 22 (Text-figs. 2–3), often some considerable distance across the temple; it is important to identify it correctly and not confuse it with 24 or 25. In *Myrsidea* seta 23 is always absent and in *Bucerophagus* it may be minute. Of the seven following marginal or submarginal setae (24–30), 29 and 30 in nearly all species can be recognized as 30 lies near and submarginal to 29, either being on the outer or on the mediad side; in *Trinoton* it is nearer seta 27; in *Numidicola* it is marginal. The next marginal seta is 28, usually short and fine; followed by 27 and 26 which are either separated or have their alveoli contiguous or nearly contiguous; in this last condition 26 is usually fine and significantly shorter than 27. The position of these two setae is a constant feature within genera and groups of genera and is a useful key character. However, it does separate *Bucerophagus*, in which 26 and 27 are closely associated, from the otherwise similar genera *Chapinia* and *Bucerocolpocephalum* Elbel in which they are not. This leaves two setae, 25 and 24, one or both of which may be minute to medium to very long; the length of these setae may be a useful character, but in *Machaerilaemus* one or both may be missing and in other genera the lengths may vary. In those species with one long and two short setae between 23 and 27 (Text-fig. 1) it is not always possible to number the long seta; it is usually submarginal to the two short marginal setae and may vary in its position relative to them. *Ancistrona* has extra setae: three long and two short between 23 and 28. In addition to these temporal setae, one of the setae anterior to 30 (here called 31) may be long and stout. The number of long setae may be generic (three in *Eomenopon*) or specific (two or three in *Kurodaia*, Price & Beer, 1963 : 851). The lengths of the head setae are not always key characters owing to the known and potential variation and to the subjective interpretation of ' long ' and ' short '.

The dorsal head sensilla may be five in number (Text-fig. 1), but there are more usually three: *a.* is not always apparent as it lies on the margin just anterior to seta 9; *b.* just posterior to 9 is useful for the identification of this seta; *c.* is usually present and associated with setae 14 and 15; *d.* associated with seta 16 and *e.* with 17 are less commonly present. The presence or absence of *e.* is a group character in *Austromenopon*, being present only in the species infesting the Alcidae; *d.* is absent in *Actornithophilus* species from the Lari, being present in species from other hosts; in

Menacanthus from the Galliformes *d.* may be present or absent in different species. The absence of *c.* may be a generic or group character: in the *Colpocephalum*-complex *c.* is usually present, but appears to be absent in the species infesting the Galliformes and in a few of those on the Ciconiiformes.

The ventral head setae are mainly constant in number and position throughout the Menoponidae. The labral setae comprise a posterior row of usually closely arranged setae and an anterior row often with 1, 3, 6 and 7 short and the remainder longer (Text-fig. 4). An examination of many species, however, shows that there is no clear distinction between ' long ' and ' short ' setae and there are many exceptions. This is not therefore usually a useful character, but in *Ancistrona* these setae are



FIGS. 4–6. 4, *Myrsidea* sp. head: *m.* 3 postmental setae; *a.* the 2 anterior subocular setae; *s.* subocular seta; *c.* subocular comb row; *d.* dorsolateral margin of head. 5, *Menacanthus stramineus*: part of venter of head; *m.* 4 postmental setae; *mp.* base of maxillary palp; *p.* postpalpal process. 6, *Trinoton* sp. antenna.

diagnostic, being all minute with the exception of one long seta each side. In all species examined there are two setae, one long and one short, at the anterior end of the ventrolateral margin (Text-fig. 4 *a*.), posterior to these are one or more setae (*s.* subocular setae, Ryan & Price, in press), followed in most genera by the subocular comb row (= lateroventral head fringe, Clay 1966 : 330). The first or only seta in group *s.* is frequently elongate and sometimes flattened and somewhat hyaline (e.g. *Eidmanniella*; Pl. 4, fig. 20); in *Meromenopon* from the Meropidae this seta is flanged with at least one tooth (Pl. 3, figs. 15–16), being unlike any other seta seen in the Mallophaga; in the congeneric species from the Coraciidae the seta is normal. The presence of only one seta in group *s.* may be a specific or generic character; in *Eomenopon* and *Pacifimenopon* the elongate seta may not be the most anterior one. In some cases it is not always possible to separate some of the setae of group *s.* from the comb row. The subocular comb row (Pl. 4, fig. 19) is characteristic of the

Menoponidae, but is absent or atypical in *Microctenia*, *Machaerilaemus* and *Ancistrona*; in the latter genus its function may have been taken over by the row of setae along the inner edge of the dorsolateral margin. In some genera (e.g. *Colpocephalum*) there is a ventral patch or line of submarginal setae on the anterior region of the temple (Pl. 4, fig. 21); this should not be confused with the subocular comb row and the seta continuous with this row which in mounted specimens may appear submarginal. In *Kelerimenopon* a band of thickening runs inwards from the ventrolateral margin with at least one seta. The histology of the setae and integument of the Menoponidae is discussed by Neuffer, 1954.

3. *The Antenna.* In all Menoponidae the antenna (Pl. 1, fig. 1) comprises the scape, pedicel and a flagellum of usually two segments, the terminal one sometimes being subdivided. The distal anterior angle of the scape and pedicel may be produced laterally (*Trinoton*) or the pedicel alone (*Mimemamenopon* Carriker) forming generic characters; the latter condition may also be only specific (*Ciconiphilus*, *Hohorstiella*). In one species of *Eidmanniella* three of the distal setae of the pedicel are broad and hyaline (Ryan & Price, in press). The first segment of the flagellum is always pedunculate or wineglass-shaped. Ferris (1923 : 57) discussing *Menopon* and Tendeiro (1967 : 384) *Chapinia*, considered that this segment was divided into two, the first being small and formed by a line across the ' stalk ', the part proximal to the line being darker in colour. This condition is apparent in many species belonging to many genera: in *Bucerophagus productus* there is no sign of an external structural division (Pl. 1, fig. 2) and no break of the internal marginal thickening; the apparent segmentation may be due only to the difference in pigmentation. In *Myrsidea cornicis* and *Pseudomenopon pilosum* in which this line is apparent, reconstructions of the antennae from sections by Buckup (1959) and Haub (1967) show no break in the pedunculate segment, these authors describing it as a single segment. It would therefore be more satisfactory to treat it as such. Kéler (1958 : 82) in the original description of *Eidmanniella* stated that the antenna appeared three-segmented as there was only a trace of the line of division between the two segments of the flagellum; stereoscan photographs of this type of antenna (Pl. 1, fig. 4) show a definite division, but perhaps not so marked as in some other species (Pl. 3, figs. 13–14). The second segment of the flagellum, usually referred to as the terminal antennal segment, may be globose to elongate, the shape frequently being similar in the species of a genus. The surface of this segment is ridged (Pl. 2, figs. 7–12) and it is these ridges when deep and in a straight line which may give a false impression of a subdivision of the segment. It is possible that the form of these ridges and the sculpturing of their edges (Pl. 1, fig. 3) may provide further taxonomic characters. The distance apart of the ridges, visible with the light microscope, has been used in the key to separate two groups (Pl. 3, figs. 13–14). The form of the sculpturing of the third segment may also prove to be a taxonomic character. Distally there are a number of setae, sometimes cone-shaped (Pl. 3, fig. 13) and two sensilla which seem to be sensilla coeloconica (Pl. 3, fig. 13; Pl. 7, fig. 42). In species with the last segment subdivided, one of these sensilla is proximal to or near the dividing line (*Cuculiphilus*, Pl. 1, fig. 3), suggesting that the primitive condition may have been a three-segmented flagellum with a sensillum on each of the two terminal segments. Whether the last

segment is subdivided or not has frequently been used as a generic character, but it now appears that this may not always be reliable. In *Cuculiphilus* there is a well marked division internally and externally (Pl. 1, fig. 3). In *Bucerophagus productus* there is an internal break in the marginal thickening and the part proximal to this is slightly more darkly pigmented, but externally there is no definite division (Pl. 1, fig. 1); one of the sensilla lies proximal to the internal division. Some species of *Menacanthus* also show a break in the internal marginal thickening of the terminal segment without any other indication of a division, so that the presence or absence of an internal break may not be relevant. It would seem that in *B. productus* the appearance of a division is partly due to the slight change in pigmentation and partly to a deep furrow between the ridges (Pl. 2, figs. 7–9). In *B. africanus* similar photographs (Pl. 2, figs. 10, 12) suggest that there is a definite division; there is also a marked difference in pigmentation in this species, the part proximal to the line of division being darker in colour. This segment in some species of *Colpocephalum* resembles that of *B. productus* in having the proximal part more darkly pigmented and the two sensilla widely separated. In *Plegadiphilus* the presence of a subdivided terminal antennal segment has again been incorrectly used as a generic character (Clay, 1947; Blagoveshtschensky, 1964). In some species of this genus the pigmentation and the ridges, together with the position of the proximal sensillum and an internal break in the marginal thickening, gives the impression of one or more subdivisions (Pl. 3, fig. 14). In *Plegadiphilus plegadis*, in which this segment is short there is no indication of a division and the two sensilla are close together. In *Austromenopon* one species (*A. affine*) shows internally and externally a line of division with the sensillum just proximal to the line, others show some indication of a line of division, while others show none. It is not possible therefore to use this character as a major division in the key.

A preliminary study of the position of the sensilla and their associated setae as possible generic characters has shown considerable variation within groups of otherwise similar species. In many species the two sensilla are near each other at the distal end of the segment and their surface apertures are similar; in *Bucerophagus* the two sensilla are widely separated and the proximal one lies in a circular pit (Pl. 2, fig. 11). *Menacanthus stramineus* has the terminal antennal segment (Pl. 3, fig. 13) typical of a number of species of *Menacanthus* from the Galliformes and Passeriformes; in this the distal sensillum is on the end surface of the segment with the majority of the setae, while the proximal is nearby with two or three setae which arise from a slight indentation. This differs from the elongated last antennal segment of *Menopon* and *Amyrsidea* in which there is no indentation and the two sensilla and the two lateral setae are close together on the end of the segment. However, other species of *Menacanthus* (that from *Arborophila*, for instance) in which the segment is elongate, the condition is similar to that of *Menopon*; and the *Menacanthus* from *Alectoris* in which the last segment is short, the sensilla are close together and the setae are merged with the group of terminal setae and no longer associated with one of the sensilla; this arrangement is also found in many of the species parasitic on the Passeriformes. Thus, the position of the sensilla is not necessarily dependent on the length of the segment; there is some indication that the wide separation of the sensilla

is associated with a tendency in the group towards subdivision of the segment. In *Austromenopon* the proximal sensillum may be near the distal end or at various positions in the distal part of the segment, being found nearest the base in *A. affine*, in which it lies near the line of division. The species of this genus probably all have two of the stout setae placed near the middle of the lateral margin of the terminal segment. It is apparent from the above survey that these characters will not provide any major divisions for the key but further studies of all the antennal characters may reveal some patterns of taxonomic interest.

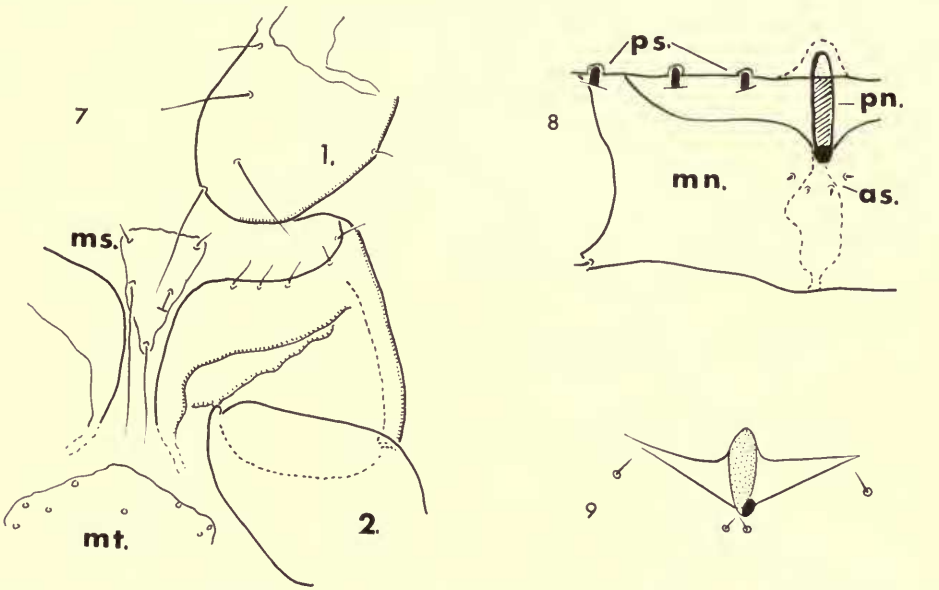
4. *Eyes*. Wundrig (1936) has shown that the Amblycera have two ommatidia each side and these show all stages from eyes with well-developed biconvex lenses (Pl. 1, fig. 6) to those with no lens. As it is doubtful whether without sections it is possible to state the exact stage of development of the ommatidia, the character of ' eyes present or absent ' has not been used. The lenses are usually located on the dorsolateral margin but in *Pseudomenopon* and part of *Eidmanniella* (new genus, Ryan & Price, in press and see Clay, 1957 : 143) the eyes are more towards the centre of the head (Pl. 1 fig. 5).

5. *Mouth Parts*. With the exception of the hypopharynx these are similar throughout the Menoponidae (Buckup, 1959; Haub, 1967). The maxillary palp is four-segmented, the last segment usually having two well-marked sub-terminal setae, the relative sizes of which may be a specific character (Clay, 1968, Pl. 1, figs. 6–7). The alveoli of these setae are usually contiguous, but may be separated by a definite gap, this appearing to be a constant character in *Dicteisia*, *Clayia* and *Somaphantus*; both conditions are found in species of *Menacanthus* parasitic on the Passeriformes. In some species these setae are not apparent and perhaps merge with the terminal setae; in *Cuculiphilus* sens. lat. there is a third seta associated with this pair (Pl. 7, fig. 45). Each labial palp has five anterior setae, in *Neomenopon* one is fine and not apparent in all specimens. The number of setae on the prementum appears to be constant; the lengths of one of these setae has been used as a species-group character in *Actornithophilus* (Clay, 1962 : 237). The postmentum usually has four setae each side; (Text-fig. 5); in a few genera (e.g. *Myrsidea*, Text-fig. 4) the most posterior seta each side is missing and in *Nosopon milvus* Tendeiro it is replaced by a clump of four to six small setae. The hypopharyngeal sclerites and the functionally associated epipharyngeal crest show various degrees of development which appear to be of little phylogenetic importance (Clay, 1962*b* : 220): otherwise similar species may have the sclerites well-developed or reduced (*Austromenopon*, Clay, 1959 : 159; *Myrsidea*, Clay, 1966, Pl. 2, figs. 1–2). In *Neomenopon* the form of the hypopharynx is unusual and may prove to be a good generic character. The distinctive epipharyngeal organs (Buckup, 1959 : 262) appear to be present in all the Menoponidae.

Thorax

Especial attention has been paid to the thorax and legs which provide many useful generic and subgeneric characters. A detailed study has been published by Mayer (1954) and only those characters of taxonomic value will be discussed here.

1. *Prothorax.* The transverse carina of the pronotum (Text-fig. 1) is apparent in all genera with the exception of *Rediella*; the vertical carina shows various stages of development. In some species there is a vertical groove each side of the pronotum giving the so-called ' winged ' or ' lobed ' prothorax. The postnotum (sens. Mayer, 1954 = mesonotum sens. Cope, 1941) in the majority of genera is a well pigmented oblong sclerite (Text-fig. 8), often distorted in mounted specimens; it may not be apparent (*Numidicola*) or it may be of a different shape (*Ancistrona*). The prosternal plate varies from being well developed to greatly reduced; in *Eidmanniella* a posterior



FIGS. 7–9. 7, *Heleonomus* sp., mesothorax: 1, 1st coxa with the 5 posterior coxal setae 2, 2nd coxa; *ms.* mesosternal plate; *mt.* metasternal plate. 8, *Colpocephalum* sp., pronotal margin and mesonotum: *ps.* pronotal marginal setae; *pn.* postnotum; *mn.* mesonotum; *as.* anterior mesonotal setae. 9, *Actornithophilus* sp., postnotum and anterior mesonotal setae.

process of the prosternal plate may be strongly or weakly sclerotized or absent. There are usually two pairs of central pronotal setae (dps) lying on or near the transverse carina, but in some species-groups (Clay, 1962 : 237) or genera (*Myrsidea*) they are reduced to one pair or absent. Although the number and lengths of the posterior marginal setae of the pronotum may be useful specific or species-group characters, they are not necessarily of generic importance. All species have two small central prosternal setae; additional setae may be of generic importance, but in some genera both conditions may be found (e.g. *Ciconiphilus, Clayia*).

2. *Mesothorax.* The mesonotum is developed to a greater or lesser extent, the differences not being sufficiently clear cut to use as a generic character. There are two different types of mesosternum: in the majority of genera (Text-fig. 7) the sclerite (part of the episternum) bearing the inner articulation of the leg is separated

from that of the other side by a distinct mesosternal plate or by an area without a definite plate. In the other type (*Myrsidea*, *Cuculiphilus*) the mesonotum, pleura and mesosternum are fused to form a sclerotized ring round the body (Clay, 1966, Pl. 1, fig. 6). The anterior mesonotal setae may be four in number clustered round the distal end of the postnotum (Text-fig. 8); in some species of *Odoriphila* the setae of the pair each side of the postnotum lie close together and in some specimens one seta may be hidden below the other giving at low power the appearance of only two. Less commonly the outer setae may be widely separated from the inner (*Actornithophilus*, Text-fig. 9) or there may be only two (*Myrsidea*). These setae are constant in position and number within genera and form useful key characters. In addition, the mesonotum has at least one other seta each side, lateral or postero-lateral to the anterior mesonotal setae, and it is important to identify these before deciding whether there are two anterior mesonotal setae or four widely spaced ones. The centre of the mesosternum usually has four or more setae, but in some genera there are only two (*Austromenopon*); this is usually a constant character within a genus or groups of genera but in *Bucerophagus* there may be two or more setae.

3. *Metathorax.* In *Myrsidea* some species may have the metanotum strongly modified while in other similar species it is normal, this character therefore seems to be of little phylogenetic importance (Clay, 1966 : 331). In *Clayia* and at least some species of *Menopon*, there is a variously developed central vertical line of thickening in the anterior part of the metanotum; however, some of the species of *Menopon* are based on specimens not in sufficiently good condition to say whether this thickening is present, but it may prove to be a good character for these two genera. The outer seta at each end of the posterior marginal or submarginal row of metanotal setae is long or the longest of the row; it is sometimes anterior to the rest of the row. The presence of many central setae on the metanotum may be a specific character (*Actornithophilus*). There is usually a central metasternal plate with setae.

The species of *Trinoton* have two large thoracic sternal plates with many setae; caudad to the posterior plate is a bilobed flap appearing white in untreated specimens (Pl. 5, fig. 25). Species of *Eureum* also have a white flap arising from what is probably the metasternum and a similar one on abdominal sternum I (Pl. 5, fig. 26) and in *Dennyus* on the metasternum and a number of the abdominal sterna. In *Trinoton* the surface sculpture (Pl. 5, figs. 28, 30) of the flap is similar in specimens parasitic on species belonging to five genera of the Anseriformes, but differs from that of the flaps in *Eureum* (Pl. 5, figs. 27, 29) and *Dennyus* (Pl. 3, fig. 17). The function of these areas is unknown. Species of *Trinoton* also have a conspicuous white area surrounding the gular plate (Pl. 5, fig. 25), but the surface sculpture is quite distinct from that of the metasternal flap (Pl. 3, fig. 18).

Legs

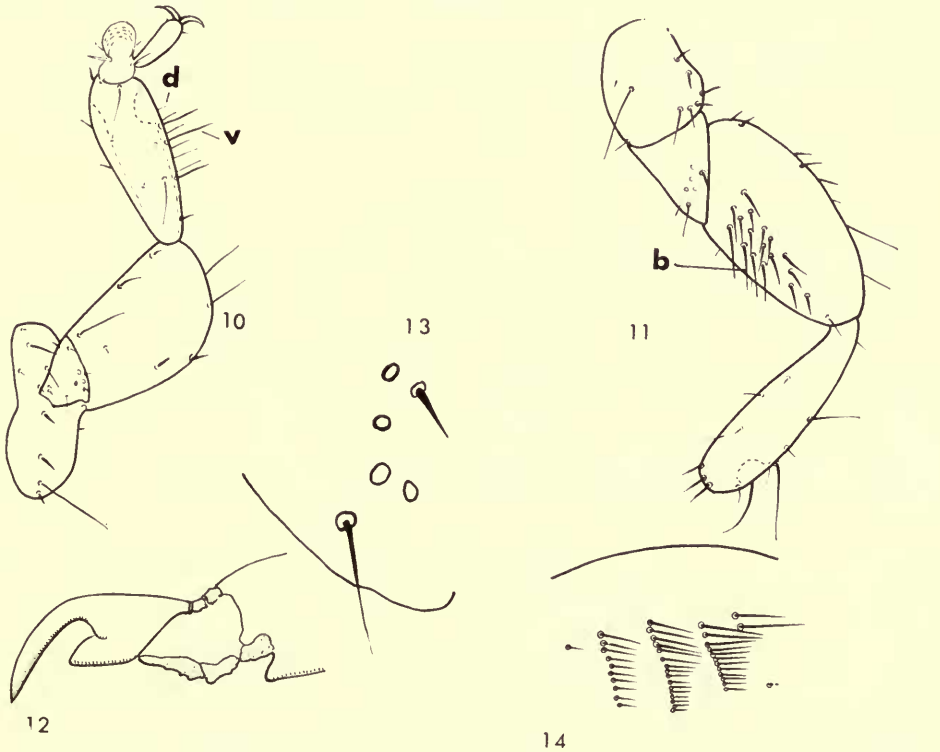
The gross morphology of the legs is similar throughout the Menoponidae (see Mayer, 1954).

1. *Coxa.* These are attached to the ventral part of the thorax except in those genera (e.g. *Trinoton*, *Eureum*) with wide sternal plates which cause the articulation

to be more lateral; in the former genus the usual anterior prolongation of the first coxa is greatly reduced. The first coxa frequently has four or five posterior setae (Text-fig. 7.), but in certain genera (*Austromenopon*) or groups of genera there are more; however some of the species may have only one or two extra setae with the occasional specimen without these (in *Eidmanniella*); this character cannot therefore always be used. Those species with many setae on coxa I may also have a greater number on II and III.

2. *Trochanter.* Ventrally there are a number of well marked sensilla associated with two setae (Text-fig. 13), the most usual number on legs II and III being four to five, but some genera (*Bonomiella*) or species-groups appear to have a constant number of three. The number is of doubtful general use in the key as it is sometimes only specific (*Nosopon*) or there is the occasional specimen in which it varies on different legs; however, in some species groups of *Menacanthus* (see below, p. 18) the number is correlated to a certain extent with other characters.

3. *Femur.* The most important taxonomic character of this segment is the ventral chaetotaxy of the third femur. This may be in the form of patches of irregularly arranged setae (brushes, Text-fig. 11) or regular rows of stout spine-like setae (combs



FIGS. 10–14. 10–11, Menoponidae legs. 10, 1st, ventral: *d.* 1st outer dorsolateral tibial seta; *v.* 2nd. outer ventrolateral tibial seta. 11, 3rd, ventral: *b.* brush of setae. 12, *Bonomiella* sp. claw. 13, Trochanter with ventral sensilla and setae. 14, Venter of 3rd femur with ctenidia.

or ctenidia, Text-fig. 14, Pl. 6, fig. 31) or a few scattered setae. The form tends to be constant throughout groups of otherwise similar species and frequently provides useful generic characters. The presence of ctenidia is a group character in the *Colpocephalum*-complex, but they are also found in other genera: *Bucerocolpocephalum* with ctenidia is otherwise similar to *Bucerophagus* and *Chapinia* without; in *Piagetiella* they may be present or absent in different species. *Microctenia*, in addition to a brush of setae, has the venter of the third femur covered with rows of comb-like outgrowths (Pl. 6, fig. 32).

4. *Tibia*. Here again the chaetotaxy shows good taxonomic characters: the number of outer dorsal setae may form useful specific characters (Clay, 1962 : 195; 1966 : 334, Text-fig. 10). Many species in which there are many outer dorsal setae on tibia I, have only a few on II and III (Text-fig. 11), while in others (*Colpocephalum*-complex) there are numerous marginal and submarginal setae in this position (Pl. 6, fig. 33). *Hoazineus* and *Heleonomus* (Pl. 6, fig. 34) have a row of short regular setae along the outer margin of I–III. In some genera the extra tibial setae may be present or absent (*Falcomenopon*, Emerson & Elbel and some species of *Kurodaia*) and in *Osborniella* the number of the tibial setae is fewer than in most species of the *Colpocephalum*-complex. There is considerable difference in the size and position of the terminal ventral tibial setae, but no clear distinctions could be found as they grade from relatively fine to thick spine-like setae and the distance between them shows all stages from two of the alveoli being contiguous to all four being widely spaced; it was decided that this is not a practical generic character. One genus (*Piagetiella*) has a tibial spur in the male.

5. *Tarsus*. Kéler (1952, 1955) and Mayer (1954) give descriptions of this joint in some species of the Menoponidae. The tarsus comprises two segments, the proximal being small and the distal being longer and of various proportions. The pretarsus bears two claws which articulate with the well-sclerotized unguifer; the shape of the claws may be diagnostic (*Bonomiella*, *Microctenia*). The unguitractor in the adult is in the form of two plates to which is attached the tendon-like apodeme of the retractor muscle of the claws, usually visible in specimens treated with KOH. Distally the dorsal part of the unguitractor may be elongated laterally forming two pointed processes (*Neomenopon*, *Hohorstiella*) or there may be a central comb-like area (*Bucerophagus*). Arising from the ventral part of the unguitractor on legs II and III is a hyaline, sometimes tuberculate process (Pl. 6, fig. 35), the empodium (sens. Kéler, 1952); the shape of this may be diagnostic (Clay, 1966); it may be small and is sometimes not apparent and perhaps absent. Owing to the difficulty of seeing its true form in mounted specimens, the empodium has not been used here as a taxonomic character. The first tarsal segment has a pair of setae usually hyaline and sometimes flattened; just distal to these is a pad-like lobe, the euplantula (sens, Kéler, 1952). Examination of sections and of the whole structure with the light and scanning electron microscopes (Pl. 7, figs. 37–41) suggests that the euplantula, in at least some species, has an outer ventral membrane covering a honey-combed area within which is a framework of vertical strands (Pl. 7, fig. 41) or of vertical and horizontal strands giving a characteristic banded appearance (Pl. 7, fig. 40). The form of these strands may be useful taxonomic characters and appears to be constant

within genera and groups of genera; all the members of the *Colpocephalum*-complex, for instance, have the vertical strands only; other genera not belonging to this complex also with vertical strands only are *Microctenia*, *Hoazineus*, *Bonomiella* and *Trinoton*. However, it is not possible to use this character for basic divisions in the key as there are a number of genera in which no internal striations can be seen and in *Menopon* it has been possible to see the striations in only some of the species. The euplantula of the second tarsal segment may be similar to that of the first (e.g. *Bucerophagus*) or show considerable differences: in some of the species in which euplantula I shows vertical striations only, II may be elongated to more than half the length of the tarsus with vertical striations and deeply serrated margins (e.g. *Turacoeca*). In this position in *Pseudomenopon* there are rows of comb-like processes (Pl. 6, fig. 35); Kéler (1952 : 581) suggested that this structure was homologous with euplantula II. Its presence enables the nymphs of *Pseudomenopon*, in which the characteristic gular plate is not developed, to be recognized generically. Examination of this area with the scanning electron microscope suggests that in some species the form of the processes may prove to be a diagnostic character. The characters of euplantula I, are probably similar on all three legs, but are usually best seen on the first leg as in mounted specimens this is more often lying in the dorsoventral plane. Pad-like structures along the inner side of the claw can be considered as pulvilli; it is not possible to say whether their degree of development is of taxonomic use. Certain other characters of the tarsus are not used owing to the difficulty of seeing them in all species or in all specimens of a species.

Abdomen

The abdomen varies greatly in shape and in those species in which the plates are not heavily sclerotized the proportions can be affected by the treatment of the specimens. The shape of the abdomen (together with the rest of the body) may be an adaptation to some particular factor of the environment, such as the inside of the quill (Clay, 1962 : 192; Tuff, 1967 : 247). A genus based on such characters might have been derived from different stocks (e.g. *Somaphantus*, see below, p. 19) and the species might have lost many of the characters showing their affinities: *Rediella* with a distinctive appearance, resembles *Actornithophilus* from the same host order in the characters of the male genitalia and the spacing of the anterior mesonotal setae.

There are six spiracle-bearing segments (III–VIII) and two (I–II) anterior to these; posteriorly to tergite VIII, there is usually a single sclerite, but some species have two. In *Myrsidea* females the terga may be strongly modified and tergite I not apparent or with II, greatly reduced in size; these modifications, as that of the metanotum, seem to be no more than specific (Clay, 1966 : 331); members of the *Colpocephalum*-complex may also show tergal modifications in the female. Sternite I is usually apparent but is not so in *Aegypiphilus*; sternites II–VI appear as discrete central plates; VII may be fused or partly fused with the following sternites to form a subgenital plate (♀ *Myrsidea*, Clay, 1966, fig. 26; *Chapinia*, both sexes) or VII may be separated from the subgenital plate (♂ *Myrsidea*, Clay, 1966, fig. 27;

Actornithophilus, both sexes); in females of the *Austromenopon* species parasitic on the Procellariformes both conditions of VII are found, so that this is not necessarily a generic character. Rarely the males show modifications of the sternites as in *Cacamenopon* Price (sternites VI–VII) and *Holomenopon goliath* Clay (sternites VIII–IX). Post vulval sclerites may or may not be apparent; their chaetotaxy is sometimes a constant and generic character (*Kurodaia* and *Nosopon*).

The pleurites are usually in the form of discrete plates separated from the sternites by a membraneous area, frequently sculptured, and from the tergites by a narrow suture. In *Piagetiella* there may be some fusion between pleurites and tergites, either sexual or specific; in the female *Myrsidea* with modified abdomens they may be reduced, absent or modified in various ways. In *Comatomenopon elbeli* the female has sucker-like organs on pleurite III. The inner posteroventral angle of some or all of the pleurites may be prolonged as a process (Text-fig. 26); this character appears to be generic in some groups (*Plegadiphilus*), but is present or absent in others (*Menacanthus* from the Galliformes). Patterns of internal thickening of the pleurites and lateral areas of the tergites may be only of specific value (in *Austromenopon* for instance) and are perhaps not useful generic characters.

The female anogenital region shows considerable variation: the typical anal corona may be present or absent in the species of *Austromenopon* parasitic on the Procellariformes (Clay & Moreby, 1967 : 158); some species of the Galliformes-infesting Menoponidae may also lack the typical anal corona and show various other modifications of the venter of the terminal segments; however, these are not always correlated with other characters showing differences and may not be of any phylogenetic significance. The lateral edges of the anus may show various setae-bearing processes which appear to be constant in certain groups and generic in character (*Turacoeca*, *Chapinia*). The male genitalia may be similar throughout a genus or genera, with the occasional species being distinct (e.g. *Menopon*). In dealing with such males and females it does not seem reasonable or useful to erect a new genus because one sex shows some unique character, while the other sex is not separable from the rest of the group. This is illustrated by the genus *Menopon* in which there is much diversity of the female anogenital region and the male genitalia. In *M. gallinae* the terminal segment of the female abdomen is elongated, the anterior (ventral) margin of the anus is widely separated from the posterior (dorsal) margin which is terminal and beset by a row of spine-like setae; in *pallens* and *interpositum* the anal margins are not so widely separated and the anus appears more normal; in *spinulosum* the last segment is not elongated, the setae surrounding the anus form a triangle, the terminal margin of the abdomen does not bear the posterior anal setae, but has a number of long and short setae. The male genitalia also show considerable difference between the typical *gallinae* form and those with the greatly enlarged and asymmetrical parameres of the *spinulosum* group.

Various structures associated with the female genital chamber (Clay, 1961, fig. 7.z; Price, 1966 : 18) and the form of the bursa copulatrix (Clay, 1968 : 207) provide useful specific and sometimes generic characters. Although the presence or absence of spermatophores in the male cannot be used as a key character it is possible that their distribution within the genera of the Menoponidae may be of taxonomic

interest. They are probably present in all *Myrsidea* (Clay, 1968 : 207) and have also been seen in species belonging to other genera (e.g. *Austromenopon*, *Ciconiphilus*, *Dicteisia*).

The spiracles usually open on the tergites, but in some species of *Myrsidea* they open on the pleurites or the membraneous area between tergite and pleurite; in *Colpocephalum heterosoma* the spiracles open on the pleurites in the female and on the tergites in the male (Price, 1965 : 128). Although the presence of crop teeth has been used as a generic character they seem to be present in all the Menoponidae: further dissections of suitable material are necessary to see whether they will show any taxonomic characters.

The Chaetotaxy of the Abdomen. All species examined have a small anterolateral seta each side of tergite I and II. At each end of the posterior row of seta, or somewhat submarginal to it, on tergites II–VIII is the post-spiracular seta with the two small associated setae (Clay, 1954 : 716); on tergite I the seta in this position is usually long and is included under the post-spiracular setae. A generally constant character is the presence or absence of a small seta laterad to each of the long outer setae on tergite I or to the post-spiracular setae on one or more tergites. Setae may be present or absent on sternite I in different species belonging to the same genus (e.g. *Myrsidea*). The presence of ctenidia on one or more sternites is usually associated with similar ones on the venter of the third femur (*Colpocephalum*-complex); in a few genera (e.g. *Piagetiella*, *Eomenopon*) there may be abdominal ctenidia but none on the femur. The position and the number and size of the setae in the sternal brushes may be a useful generic character.

Part II

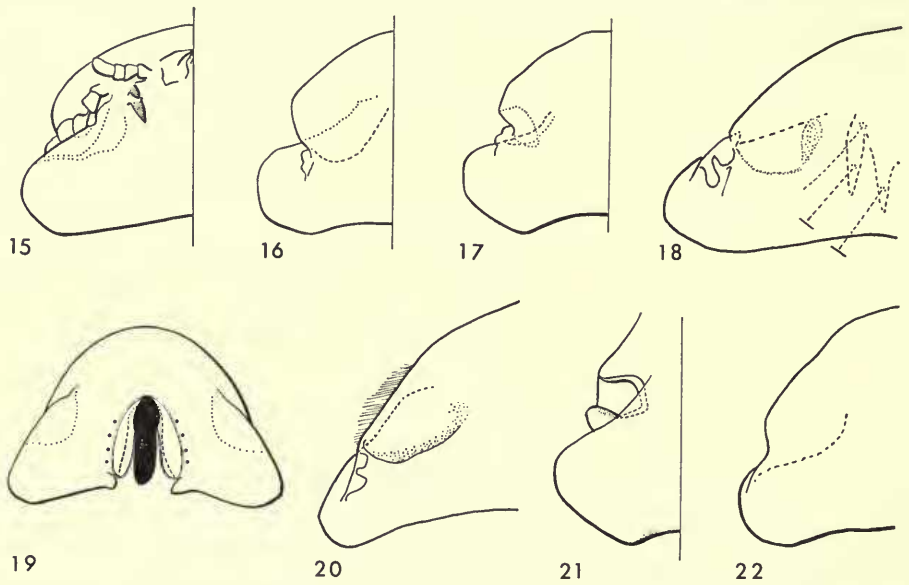
KEY

INTRODUCTION

The key includes all the generally recognized genera and subgenera (with the exception of those belonging to the *Colpocephalum*-complex and the *Menacanthus*-complex) even where it is considered that there is no advantage in the recognition of some of these taxa. The *Colpocephalum*-complex, as interpreted here, comprises all those genera with ctenidia on the venter of the 3rd femur with the exception of *Cuculiphilus* sens. lat., *Bucerocolpocephalum*, *Piagetiella*, *Turacoeca* and *Odoriphila*; it is possible that the last genus should be included. *Dicteisia* may belong to the complex but is separated in the key. Other characters common to the complex are the contiguous alveoli of head setae 26 and 27; setae 24 and 25 are usually minute to short, in a few species they are longer, but do not reach to the end of the pronotum; the presence of a vertical patch of submarginal setae on the temples; head sensilla *c.* usually present; four anterior mesonotal setae; usually more than two central mesosternal setae; mesosternum normal; tibiae II–III usually with submarginal patch or row of outer distal dorsal setae, euplantula with vertical striations only; ctenidia on one or more sternites. Balter (personal communication and see Balter, 1968) has found that the operculum of the egg opens diagonally in species of the complex from the Galliformes, Falconiformes, Ciconiiformes, Pelecaniformes,

Psittaciformes and Passeriformes; in addition this character is found in the eggs of *Nosopon*, but not of *Osborniella* or any of the species of *Ciconiphilus* examined.

The *Menacanthus*-complex comprises *Menacanthus*, *Amyrsidea*, *Argimenopon* Eichler, *Cracimenopon* Carriker and *Desumenopon* Carriker, its species being parasitic mainly on the Galliformes and Passeriformes. Divisions within this complex are dependent on which characters are used, these include: width of head and form of its dorsolateral margin; form of gular and prosternal plates; development of the hypopharynx; presence of postpalpal processes; shape of the antennal segments; number of setae on coxa I; number and position of the sternal brushes of setae; presence of sternal spiniform setae; position of the post-spiracular setae on tergites I–II; degree of development of the internal tergal and pleural thickening; presence of a prolongation of the posteroventral corner of the pleurites; terminal segments of the female abdomen and the male genitalia. A distinctive species group (including



FIGS. 15–22. Heads of Menoponidae genera. 15, *Odoriphilia*. 16, *Neomenopon*. 17, *Meromenopon*. 18, *Colimenopon*. 19, *Pseudomenopon*. 20, *Ancistrona*. 21, *Dennyus*. 22, *Gruimenopon*.

the type species of *Menacanthus*) parasitic on the Passeriformes has long postpalpal processes; an approximately rectangular, strongly pigmented gular plate with or without a central thinner area; two to four setae anterior to the subocular comb row; three ventral sensilla on the trochanter; and spiniform setae laterally on the posterior margin of the sternites. Another group (e.g. *M. alaudae*), also parasitic on the Passeriformes, has short postpalpal processes; gular plate various; four to five setae anterior to the comb row, two of which are long; four ventral sensilla on the trochanter; and no spiniform setae on the sternites. This group, in addition to being found on the Passeriformes, is found on the Picidae (the species may have

fewer setae anterior to the comb row and rather longer head processes) and on the Galliformes (length of processes varies). Amongst other species parasitic on the Passeriformes are those showing characters intermediate between the two groups: a species from one of the Parulidae has the characters of the first group but the post-palpal processes are small; *Menacanthus crateropus* has shorter processes than in the first group, no sternal spiniform setae, three setae anterior to the comb row and three sensilla on the trochanter; the species on *Salpinctes* (Troglodytidae) has small processes, four to five setae anterior to the comb row; no sternal spiniform setae and three sensilla on the trochanter. Elsewhere (Hopkins & Clay, 1955 : 180) the possibility has been discussed that some of the species of *Menacanthus* from the Galliformes are nearer to species of *Amyrsidea* than to other species included in *Menacanthus*, being separable only by the presence of the postpalpal process.

It is possible that *Menopon*, *Clayia* and *Somaphantus* also belong to the *Menacanthus*-complex. It has already been suggested that the species of *Somaphantus* might be derived from more than one Galliformes-infesting stock, the similarity being due to the environment of the quill inside which they live. This would explain some of the differences between the species such as the position of the post-spiracular setae and chaetotaxy of the head; *spencei* Emerson is the only species with a circular structure within the genital chamber. *S. kingi* Emerson and Price (no specimens seen) resembles other species of *Somaphantus* in the tubular abdomen, but differs in the number of the sternal brushes and does not have the typical *Somaphantus* head; its affinities lie perhaps with such species as *Amyrsidea elbeli* Emerson and Stojanovich; the female of this latter species resembles *Menopon gallinae* in the prolongation of the last segment and the form of the anus. *S. kingi* is not included in *Somaphantus* in the key.

These genera of Menoponidae found on the Galliformes are possibly derivatives from a single ancestral stock perhaps parasitic on an early Galliformes stock; the evolution of the parasites may have included not only divergence with the divergence of their hosts but also perhaps secondary infestations from host to host at the specific and supra-specific level.

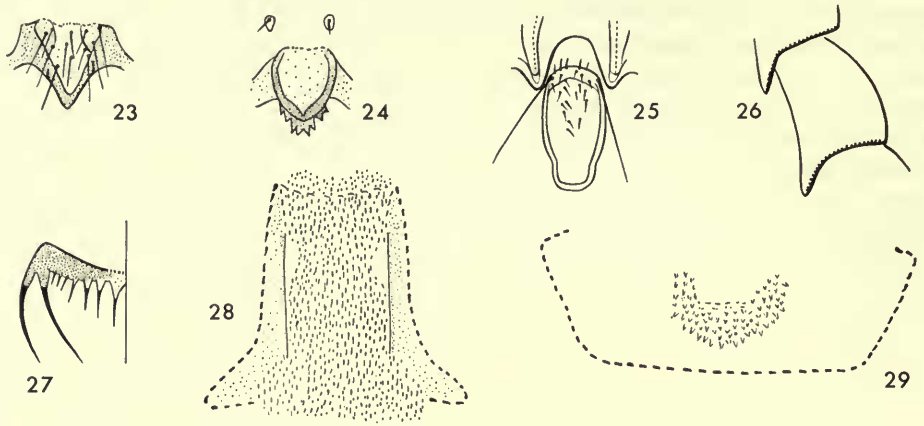
Notes

Illustrations. In preparation of this paper use has been made of the Stereoscan scanning electron microscope (S.E.M.) and this has made possible the elucidation of certain structures. Although most of these can be seen with the light microscope, especially when once identified and elucidated with the scanning electron microscope, photographs taken with this latter instrument are the most accurate method of representing small structures.

Authors and Bibliographical References. In order to save space authors of genera and species appearing in Hopkins & Clay, 1952, 1953, 1955 are not cited and only those references which do not appear in Kéler, 1960 are listed. Published works consulted but not always acknowledged in detail are the excellent series of papers on the genera of the *Colpocephalum*-complex by Price *et alia*.

Supplementary Characters. These are separately paragraphed in the key; they are further attributes characteristic of the genus or group of genera and may help to

confirm the correct placing of the specimen being identified. New species anomalous in respect of the key characters may still be placed in the correct genus; the key is an artificial arrangement and should be made to fit the genus not the genus to fit the key.



FIGS. 23–29. 23–24, Prosternal plates. 23, *Machaerilaemus*. 24, *Holomenopon*. 25, *Eureum*, prosternal and part of gular plate. 26, *Plegadiphilus*, abdominal pleurites III-IV. 27, *Turacoeca*, ventral margin of ♀ anus. 28–29, Microtrichial patch in ♀ genital chamber. 28, *Cuculiphilus* (*Falcophilus*). 29, *Cuculiphilus* (*Cuculiphilus*).

Actornithophilus and Longimenopon. These are placed together in the key, couplet 49, as it seems probable that the species of *Longimenopon* will prove to be generically inseparable from those included in *Actornithophilus* (see Timmermann, 1965 : 179).

KEY TO GENERA OF THE MENOPONIDAE

1		Alveoli of marginal temporal setae 26 and 27 closely associated (Text-figs. 2–3)	2
–		Alveoli of marginal temporal setae 26 and 27 not closely associated (Text-fig. 1)	30
2	(1)	Head seta 26 similar to 27, long and proximally stout. Mandibles each with 3–4 teeth, some posteriorly tuberculate; deep narrow preocular slit; prosternum with > 2 central setae; ♂ with tibial spur; 3rd femur with or without ctenidia; one or more sternites with ctenidia; large species, length > 3·8 mm . . . . . ***PIAGETIELLA***	
–		Head seta 26 significantly shorter and finer than 27 (Text-fig. 2) . . .	3
3	(2)	Venter of 3rd femur with ctenidia (Text-fig. 14) Setae 24–25 short to medium	4
–		Venter of 3rd femur without ctenidia	8
4	(3)	Sternites without ctenidia; no preocular notch or slit. Each side of ♀ tergite VI comb of elongate setae with clubbed ends held in pocket in tergite VIII . . . . . NEW GENUS (in press)	
–		One or more sternites with ctenidia; preocular notch or slit	5
5	(4)	2 postpalpal processes each side (Text-fig. 15) Narrow preocular slit; prosternum with > 2 central setae; 4 anterior mesonotal setae; sternites III-IV with single full ctenidium each side ***ODORIPHILA***	

– Without 2 postpalpal processes each side 6

6 (5) 2 anterior mesonotal setae; ventral margin of ♀ anus with 2 processes each end, each bearing long spine-like setae (Text-fig. 27).
Occipital setae (21–22) minute, seta 23 long and lateral to 22; broad shallow preocular notch; single ctenidium each side of sternites III–IV or III–V
TURACOECA

– 4 anterior mesonotal setae; ♀ anus without ventrolateral processes.
Euplantula with vertical striations only 7

7 (6) Typical oblong strongly pigmented postnotum absent.
Seta 20 medium length, longer than 19; > 2 prosternal setae; pronotum with scattered minute setae; sternite III-IV with single full ctenidium each side
DICTEISIA

– Typical oblong strongly pigmented postnotum present ***COLPOCEPHALUM*-complex** p. 17

8 (3) 2 anterior mesonotal setae 9

– 4 anterior mesonotal setae 11

9 (8) Prosternal plate well-developed, pointed posteriorly (Text-fig. 23) prosternum with > 2 central setae.
Antennal fossa deep, head broad at temples and preocular expansions; 3rd femur without brush; trochanter with not more than 3 ventral sensilla
MACHAERILAEMUS

– Prosternal plate not well developed and not pointed posteriorly; prosternum with 2 central setae
Seta 23 missing or anterior to 22 10

10 (9) Proximal antennal sensillum large, in pit and widely separated from distal (Pl. 2, figs. 10–11); claw without large basal process; bilobed process each end of ♀ ventral anal margin with long setae, some of which may be stout and spiniform; temples expanded; euplantula banded; trochanter with more than 3 ventral sensilla.
Seta 23 missing or minute; 3rd femur with or without brushes
BUCEROPHAGUS

– Antennal sensilla small, adjacent and terminal; claw with large basal process (Text-fig. 12); ♀ anus without ventral processes; temples scarcely expanded; euplantula not banded; trochanter with 3 ventral sensilla.
3rd femur without brushes; seta 24–25 short. . . ***BONOMIELLA***

11 (8) Tibiae I-III with outer submarginal comb of short setae (as in Pl. 6, fig. 34); brushes on sternite IV-V towards centre of segments.
Preocular slit; terminal antennal segment elongate, cylindrical; 3rd femur with thick brushes; euplantula with vertical striations only; setae 24–25 short . . . . . ***HOAZINEUS***

– Tibiae I-III without such comb of setae; brushes or ctenidia on sternites IV-V absent or lateral on segments 12

12 (11) Gular plate large and tripartite (Text-fig. 19); 2nd tarsal segment of 2nd and 3rd legs with combs of processes (euplantula II, Pl. 6, fig. 35).
Seta 24 or 25 long; preocular slit; postpalpal processes present or absent; some abdominal pleurites with posteroventral corners prolonged
PSEUDOMENOPON

– Gular plate and tarsi not as above 13

13 (12) Gular plate with 4 seta-bearing processes (Text-fig. 18).
Seta 24 or 25 long; head considerably broader than long; antennal fossa deep and pouch-like; prosternal plate with posterior process and > 2 setae; tergites I & II with short seta laterad to post-spiracular seta ***COLIMENOPON***

– Gular plate without 4 seta-bearing processes 14

14 (13) One spinous process near base of antenna and one near base of maxillary palp; thickening running inwards from anterior end of subocular comb row bearing at least one seta.
Close set row of subocular setae; head sensilla *c.* not apparent; tergite I with short seta laterad to post-spiracular seta; euplantula banded; seta 24–25 short . . . . . (***KELERIMENOPON***) 15

– Head without such spinous processes and without setae-bearing thickening running inwards from comb row 16

15 (14) Abdominal pleurites without prolongation of ventro-posterior corner; broad deep preocular notch . . . . . sg. ***LORIMENOPON*** Price & Emerson

– Some abdominal pleurites with prolongation of ventro-posterior corner; narrow preocular slit . . . . . sg. ***KELERIMENOPON***

16 (14) Labrum with striated lobe (Pl. 4 fig. 23); hypopharynx characteristic (Pl. 4, fig. 22).
Head broad, dorsal preocular margin overlapping ocular margin (Text-fig. 16); sensilla *c.* not apparent; setae 24–25 short . . ***NEOMENOPON***

– Labrum without striated lobe; hypopharynx not as in Pl. 4, fig. 22 . . 17

17 (16) Dorsum of head with scattered minute alveoli
♀ with 1–2 circular or oval structures associated with genital chamber; setae 24–25 short 18

– Dorsum of head without scattered minute alveoli 20

18 (17) Distal anterior angle of pedicel not markedly prolonged; posterior part of coxa I with > 6 setae; single structure in ♀ genital chamber; ♂ genitalia asymmetrical.
Head semilunar 19

– Distal anterior angle of pedicel markedly prolonged; posterior part of coxa I with < 6 setae; 2 oval structures in ♀ genital chamber; ♂ genitalia symmetrical . . . . . ***MIMEMAMENOPON***

19 (18) Sternite I divided vertically, partially or entirely; gular plate sculptured; prosternum with only 2 central setae . . . . ***EOMENOPON***
Sternite I not divided; gular plate not sculptured; prosternum with > 2 central setae . . . . . ***PACIFIMENOPON***

20 (17) Venter of 3rd femur without brushes; temples with ventral submarginal patch or row of setae; setae 24–25 short; postvulval sclerite with setae; head broad at temples, semilunar . . . . . ***NOSOPON***

– Without above combination of characters 21

21 (20) One postpalpal process each side; seta 24–25 short
Sensilla *c.* not apparent; prosternal plate with well-developed posterior process or with 3 irregular small processes 22

– Either without postpalpal processes or if present then seta 24 or 25 long . . 23

22 (21) Head without preocular slit or notch; pleurites without prolongation of posteroventral corners; tergite I without short seta laterad to post-spiracular seta; well-developed circular structure of cellular appearance associated with ♀ genital chamber . . . . . ***APTERYGON***

– Head with preocular slit; some pleurites with posteroventral prolongations; tergite I with short seta laterad to post-spiracular seta; either no or different type of structure associated with ♀ genital chamber . . ***HOHORSTIELLA***

23 (21) 3 or more preocular setae (10–11) on at least one side; tibiae II-III with patch or row of outer dorsal submarginal setae; dorsal preocular margin overlaps ocular margin (Text-fig. 17).
Head sensilla *c.* not apparent; euplantula banded; seta 24–25 short ***MEROMENOPON***

– Without above combination of characters 24

24 (23) Postnotum not apparent; head seta 16–19 all long and stout, reaching at least to the transverse pronotal carina.
Seta 24 long and stout; no preocular notch or slit . . ***NUMIDICOLA***
– Postnotum present; head seta 16–19 not as above. 25
25 (24) Brushes on sternite IV only.
No setae between 23 and 27 reaching beyond transverse pronotal carina . 26
– Brushes absent or not on sternite IV only 27
26 (25) The 2 subterminal setae of maxillary palp with definite gap between their alveoli; shape of head characteristic (Pl. 7, fig. 44); abdomen narrow and tubular . . . . . ***SOMAPHANTUS***
– The 2 subterminal setae of maxillary palp with their alveoli contiguous; shape and head of abdomen otherwise . . . . . ***MENOPON***
27 (25) Inner central pronotal setae absent or on posterior part of pronotum; no seta between 23 or 27 reaching beyond transverse pronotal carina.
Broad or shallow preocular notch . . . . . ***CLAYIA***
– Inner central pronotal setae on or near transverse carina; one seta between 23 and 27 reaching below transverse pronotal carina 28
28 (27) Terminal antennal segment without signs of division; ridges numerous and close together (Pl. 3, fig. 13) . . . ***MENACANTHUS*-complex**, p. 18
– Terminal antennal segment with form of ridges and pigmentation suggesting one or more divisions, or if no signs of division, ridges are few and widely separate (Pl. 3, fig. 14) 29
29 (28) More than 2 central prosternal setae; pleurites without posterior processes; tergites with transverse bar . . . . . ***EUCOLPOCEPHALUM***
– Only 2 central prosternal setae; some abdominal pleurites with posterior processes; no transverse tergal bars . . . . . ***PLEGADIPHILUS***
30 (1) Thorax with 2 large sternal plates bearing many setae (Pl. 5, fig. 25); scape (and pedicel) with distal anterior prolongations (Text-fig. 6).
Seta 11 on protuberance; large species, length > 4·00 mm . ***TRINOTON***
– Thorax without such sternal plates; scape without distal anterior prolongation 31
31 (30) 2 anterior mesonotal setae.
Seta 23 absent or anterior to 22; at least one of the setae 24, 25 or 26 long; sensilla *c.* not apparent; euplantula banded 32
– 4 anterior mesonotal setae (sometimes widely spaced) 36
32 (31) One pair of mid-dorsal head setae; not more than one pair of central pronotal setae; no preocular slit or notch; ♀ ventral anal margin without lateral setae-bearing processes 33
– Two pairs of mid-dorsal head setae; 2 pairs of central pronotal setae; preocular slit or notch; ♀ ventral anal margin with lateral setae-bearing processes . 35
33 (32) Prosternum with 2 central setae; dorsal margin of head without ventral truncated ovoid excavation; seta 23 absent; no central pronotal setae.
Mesothorax with sternum, pleura and tergum fused to form strongly pigmented ring . . . . . ***MYRSIDEA***
– Prosternum with > 2 central setae; ventral truncated-ovoid excavation in dorsal margin of head with thickened anterior rim; seta 23 present; one pair of central pronotal setae 34
34 (33) Gular plate horseshoe-shaped (Text-fig. 25); temporal carina not developed ***EUREUM***
– Gular plate not horseshoe-shaped; temporal carina well developed ***DENNYUS***
35 (32) Venter of 3rd femur and sternite IV with ctenidia; terminal antennal segment with signs of division; ♀ anal processes with stout spiniform setae ***BUCEROCOLPOCEPHALUM***
– Venter of 3rd femur and sternite IV without ctenidia; terminal antennal segment without signs of division; ♀ anal processes with long setae . ***CHAPINIA***

36 (31) Venter of 3rd femur and lateral areas of some sternites with comb-like outgrowths (Pl. 6, fig. 32); distal tarsus swollen; claws delicate with narrow elongate points (Pl. 6, fig. 36).
Euplantula with vertical striation only; postnotum not vertically oblong; preocular notch . . . . . ***MICROCTENIA***

– Venter of 3rd femur and lateral areas of sternites without comb-like out growths; tarsi and claws not as above 37

37 (36) Centre of mesosternum with 2 setae.

– Tergite I with short seta laterad to post-spiracular setae, may be lacking in *Austromenopon becki* 38

– Centre of mesosternum with > 2 setae.
Seta 23 missing or anterior to 22; sternal brushes absent or only on, or thickest on IV 47

38 (37) Mesothorax as a sclerotized ring formed by fused sternum, pleura and tergum; temples with ventral submarginal patch or rows of setae.
Seta 18 widely posterolateral to 17; group of 3 subterminal setae on maxillary palp (Pl. 7, fig. 45); terminal segment of antenna subdivided (Pl. 1, fig. 3); head broad with narrow preocular slit 39

– Mesothorax not fused as above; temples without ventral submarginal patch or rows of setae 43

39 (38) Venter of 3rd femur without ctenidia; tergites I-VII with short seta laterad to post-spiracular seta . . . . . NEW GENUS (in press)

– Venter of 3rd femur with ctenidia; tergites III-VII without short seta laterad to post-spiracular seta.
Euplantula with vertical striations only . . (***CUCULIPHILUS***) 40

40 (39) Postpalpal processes present . . . . . sg. ***CARRIKERIA***

– Postpalpal processes absent 41

41 (40) Abdominal sternite I not apparent . . . . . sg. ***AEGYPIPHILUS***

– Abdominal sternite I apparent 42

42 (41) ♀ genital chamber with vertically elongate patch of microtrichia and with sclerite each side with thickened inner margin (Text-fig. 28); ♂ with stout spiniform setae on tergite VII . . . . . sg. ***FALCOPHILUS***

– ♀ genital chamber with patch of microtrichia not vertically elongate and without such sclerite each side (Text-fig. 29); ♂ without spiniform setae on tergite VII . . . . . sg. ***CUCULIPHILUS***

43 (38) Narrow preocular slit.
Euplantula banded 44

– Without preocular slit.
Seta 23 anterior to 22 45

44 (43) Eyes in normal position on dorsolateral margin; dorsolateral and ventrolateral margins normal (Pl. 4, fig. 19); seta 23 in line with 22 and 21; tibiae II and III with 1–2 irregular submarginal rows of dorsal setae; tergite II without short seta laterad to post-spiracular seta. . . NEW GENUS Ryan & Price in press

– Eyes not marginal (Pl. 1, fig. 5); cavity between dorsolateral and ventrolateral margins roofed over distally (Pl. 4, fig. 20); seta 23 anterior to 22; tibiae II and III without extra rows of dorsal setae; tergite II with short seta laterad to post-spiracular seta . . . . . ***EIDMANNIELLA***

45 (43) Large triangular or rectangular postnotum; dorsolateral margin of head with row of short setae.
No typical subocular comb row; only one of labral setae long each side; 2 short and 3 long setae between setae 28 and 23; venter of 3rd femur without brushes . . . . . ***ANCISTRONA***

– Normal vertically oblong postnotum; dorsolateral margin of head without row of short setae 46

46 (45) Prosternal plate with deeply serrated margin (Text-fig. 24); tergite II with short seta laterad to post-spiracular seta . . . . . ***HOLOMENOPON***

– Prosternal plate without deeply serrated margin; tergite II without short seta laterad to post-spiracular seta . . . . . ***AUSTROMENOPON***

47 (37) Tibiae I-III with dorsal row or rows of short stout submarginal setae, significantly shorter than outer ventral setae.
At least one long stout seta between 27 and 23 48

– Tibiae I-III without such setae.
Anterior mesonotal setae separated 49

48 (47) Outer dorsal tibial setae in comb-like row (Pl. 6, fig. 34); head narrowed anteriorly; preocular notch backed by heavily pigmented nodus (Pl. 4, fig. 24) ***HELEONOMUS***

– Outer dorsal tibial setae in irregular row or rows; head broadly rounded anteriorly; preocular concavity without heavily pigmented nodus (Text-fig. 22) ***GRUIMENOPON***

49 (47) Without typical pronotal transverse carina or typical oblong postnotum.
Head narrow, elongate, sides approximately parallel without notch or slit (Pl. 7 fig. 43); terminal antennal segment with signs of division; vertical carina of pronotum well-developed; 3rd femur without brushes . ***REDIELLA***

– Transverse pronotal carina and postnotum typical.
Euplantula banded . ***ACTORNITHOPHILUS & LONGIMENOPON***

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PLATE 1

FIG. 1. *Bucerophagus productus*. Antenna.
FIG. 2. *Bucerophagus productus*. Base of 3rd antennal segment.
FIG. 3. *Cuculiphilus snodgrassi*. 4th and 5th antennal segments.
FIG. 4. *Eidmanniella* sp. n. (in press). 3rd and 4th antennal segments.
FIG. 5. *Eidmanniella* sp. n. (in press). Dorsum of head.
FIG. 6. *Plegadiphilus* sp. Dorsum of head. *o*. ommatidia; *d*. dorsolateral margin of head.

(S.E.M.)

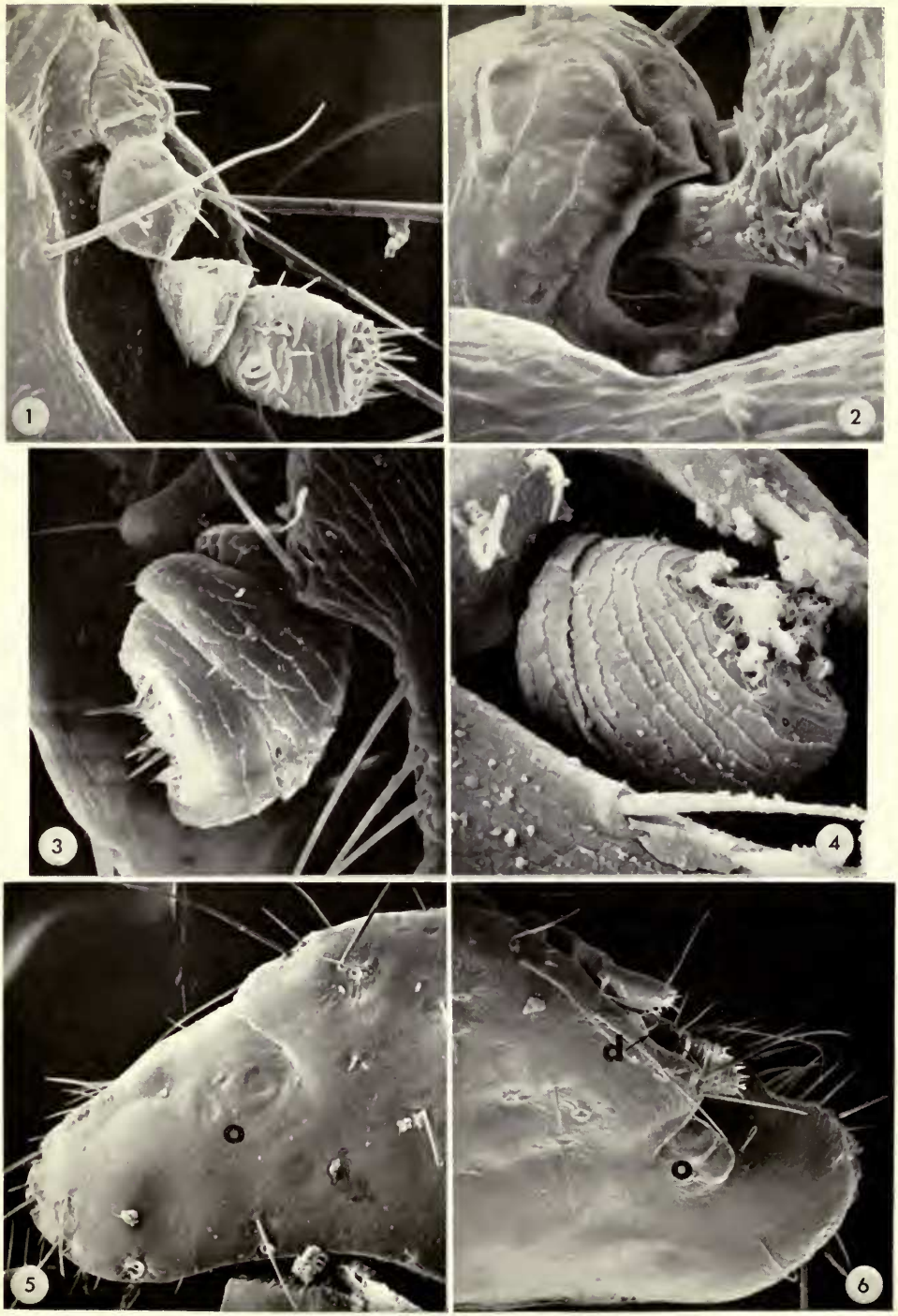

1
2
3
4
o
5
d
o
6

PLATE 2

FIGS. 7–12. *Bucerophagus antenna* (S.E.M.). *x*. marks the same seta in figs. 7–9; *y*. the same seta in figs. 10–12.

FIG. 7. *B. productus*. Terminal antennal segment.

FIG. 8. *B. productus*. End-on view of terminal antennal segment.

FIG. 9. *B. productus*. As fig. 2, enlarged.

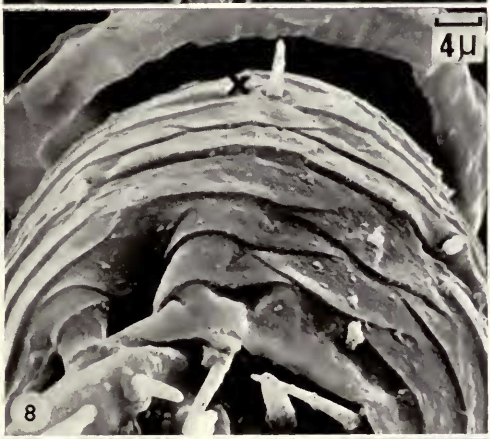
FIG. 10. *B. africanus*. Antenna.

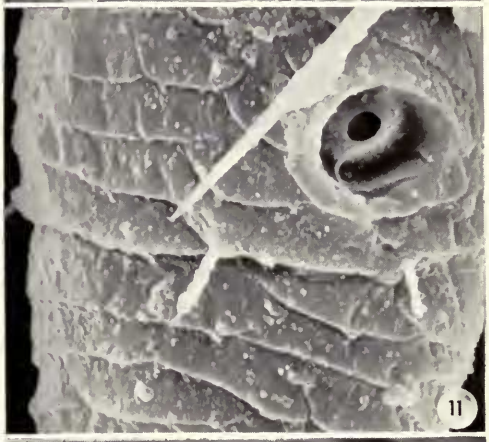
FIG. 11. *B. africanus*. Part of terminal segment showing proximal sensillum.

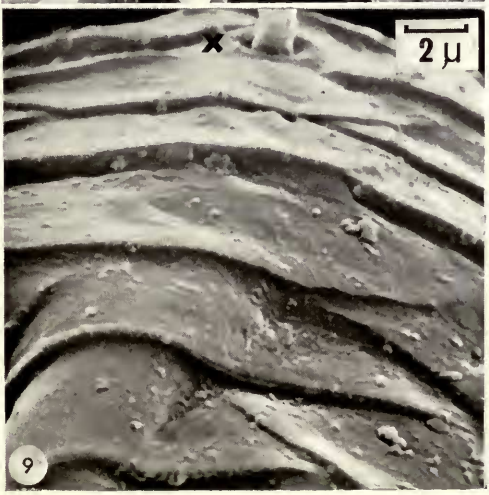
FIG. 12. *B. africanus*. Part of terminal antennal segment. (S.E.M.)


12 µ
x
7


y
10


4µ
x
8

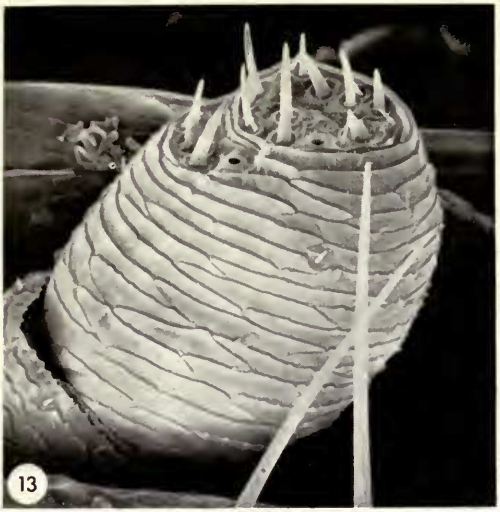

11


x
2 µ
9


y
12

PLATE 3

FIG. 13. *Menacanthus stramineus*. Terminal antennal segment.
FIG. 14. *Plegadiphilus* sp. from *Geronticus eremita*. Terminal antennal segment.
FIGS. 15–16. *Meromenopon* sp. To show variation (not specific) in subocular seta (*s*).
FIG. 17. *Dennyus* sp. Details of metasternal flap.
FIG. 18. *Trinoton emersoni* Clay. Part of white gular area with 2 gular setae. (S.E.M.)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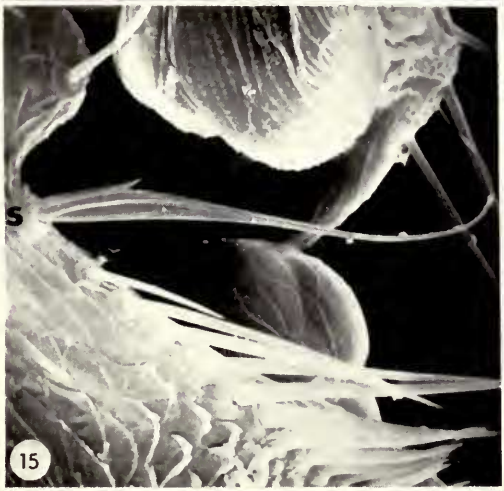
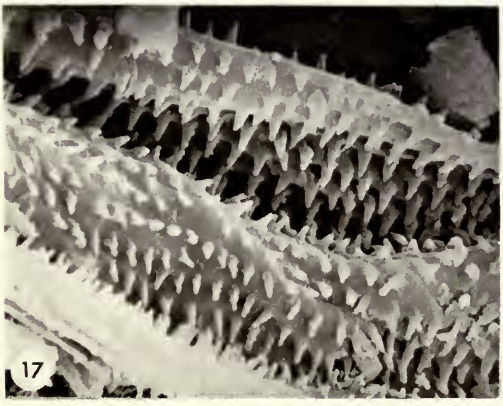
14


S
15


S
16


17


18

PLATE 4

FIG. 19. *'Eidmanniella' aurifasciata*. Antennal fossa. *s*. subocular seta; *c*. subocular comb row. (S.E.M.)

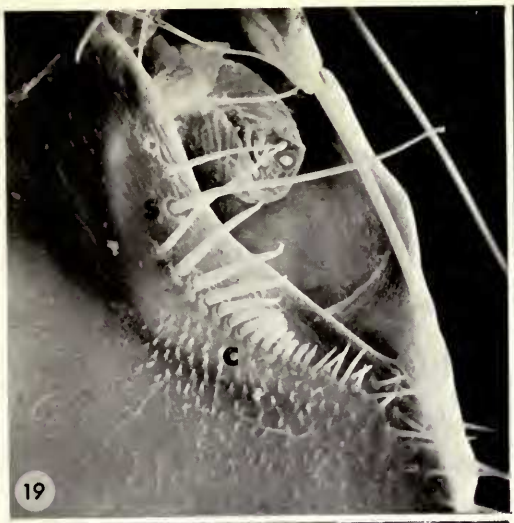
FIG. 20. *Eidmanniella* sp. Antennal fossa. (S.E.M.)

FIG. 21. *Colpocephlaum* sp. *c*. subocular comb row; *t*. submarginal temporal setae. (S.E.M.)

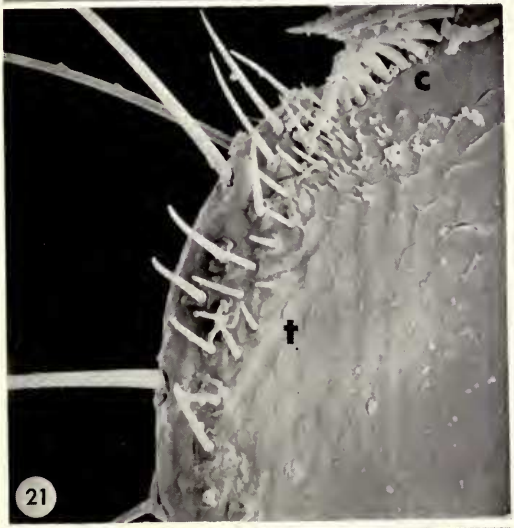
FIG. 22. *Neomenopon* sp. Hypopharynx. (Light microscope. T.C.)

FIG. 23. *Neomenopon* sp. Labrum. (Light microscope. T.C.)

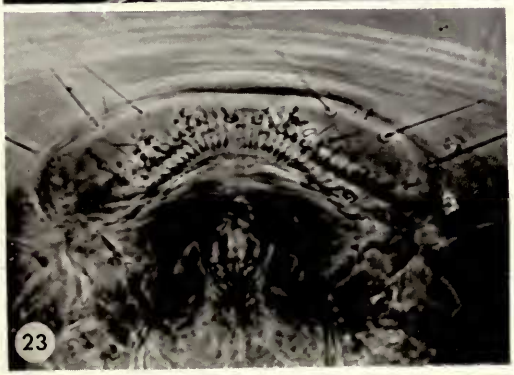
FIG. 24. *Heleonomus* sp. Head. (Light microscope. T.C.)


c
19


20


c
t
21


22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24

PLATE 5

FIG. 25. *Trinoton querquedulae*. *g*. white gular area; *m*. metasternal flap. (Direct illumination. T.C.).

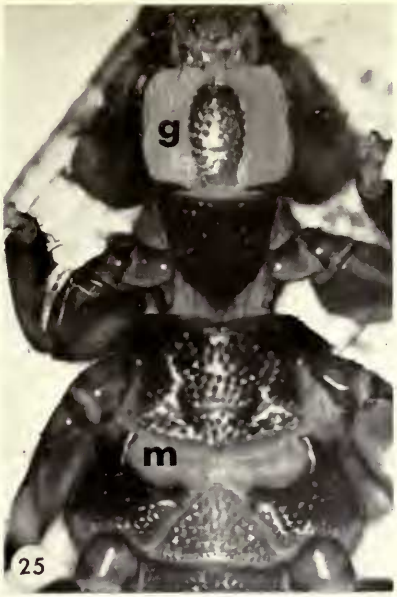
FIG. 26. *Eureum cimicoides*. Venter of thorax and part of abdomen. *m*. metasternal flap (S.E.M.)

FIG. 27. *Eureum cimicoides*. Metasternal flap. (S.E.M.)

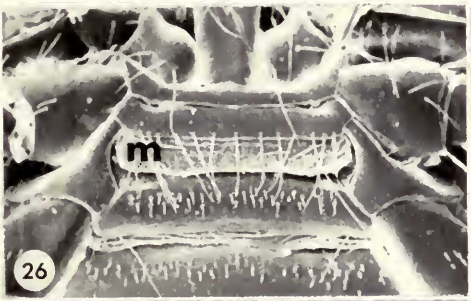
FIG. 28. *Trinoton* sp. Part of metasternal flap. (S.E.M.)

FIG. 29. *Eureum cimicoides*. Details of metasternal flap (S.E.M.)

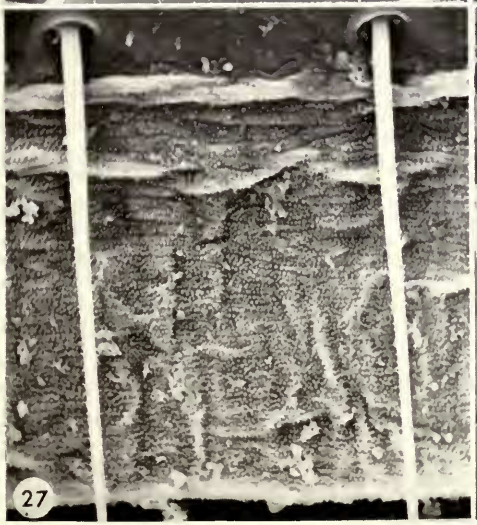
FIG. 30. *Trinoton* sp. Details of metasternal flap (S.E.M.)


g
m
25


28


m
26


3 µ
29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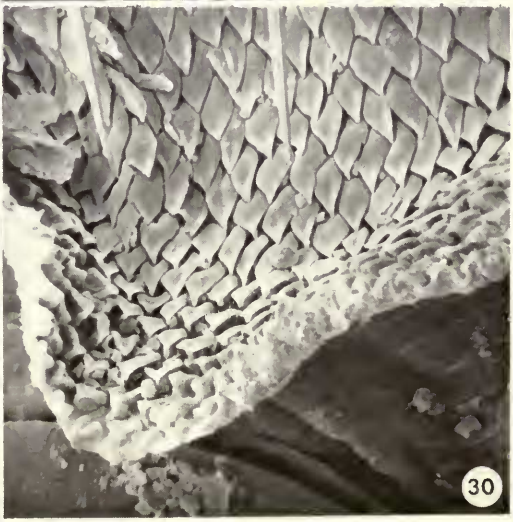
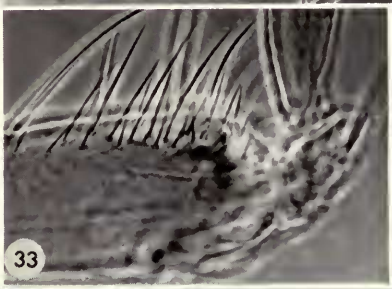

30

PLATE 6

FIG. 31. *Colpocephalum* sp. Femoral ctenidia. (S.E.M.)
FIG. 32. *Microctenia* sp. Femoral comb-like processes. (S.E.M.)
FIG. 33. *Franciscoloa roseicapillae* Price & Beer. 3rd tibia (Phase contrast T.C.)
FIG. 34. *Heleonomus* sp. Row of setae on outer tibial margin. (S.E.M.)
FIG. 35. *Pseudomenopon pilosum*. Euplantula II. *e*. base of eupodium; *d*. piece of dirt. (S.E.M.)
FIG. 36. *Microctenia* sp. Tarsus. (Phase contrast. T.C.)


31


5μ
32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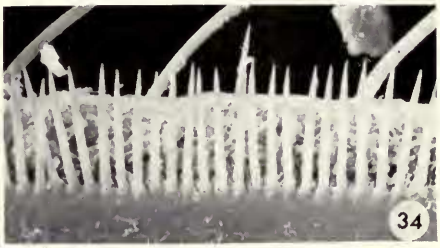

34


e
d
35


36

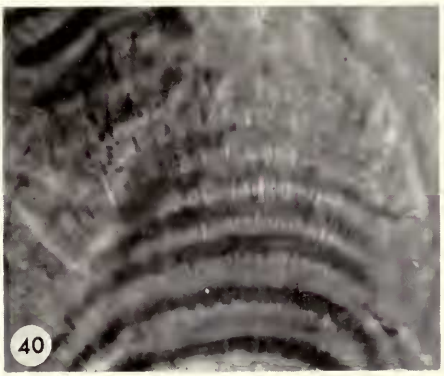
PLATE 7

FIG. 37. *Amyrsidea* sp. Euplantula I. (S.E.M.)
FIG. 38. *Actornithophilus* sp. Euplantula I. ? without surface membrane. (S.E.M.)
FIG. 39. Part of fig. 2, enlarged (S.E.M.).
FIG. 40. *" Eidmanniella " aurifasciata.* Euplantula I, to show horizontal banding. (Phase contrast. T.C.)
FIG. 41. *Falcomenopon* sp. Euplantula I, to show vertical striations. (Phase contrast. (T.C.)
FIG. 42. *Plegadiphilus* sp. Proximal sensillum. (S.E.M.)
FIG. 43. *Rediella mirabilis.* Head. (T.C.)
FIG. 44. *Somaphantus spencei.* Head. (T.C.)
FIG. 45. *Cuculiphilus snodgrassi.* Subterminal sensory setae of maxillary palp. (S.E.M.)


37


38


39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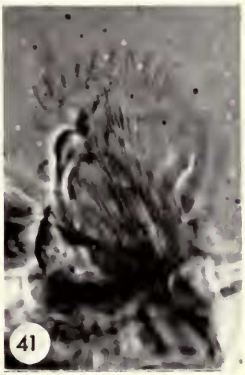
41


2μ
42


43


44


45